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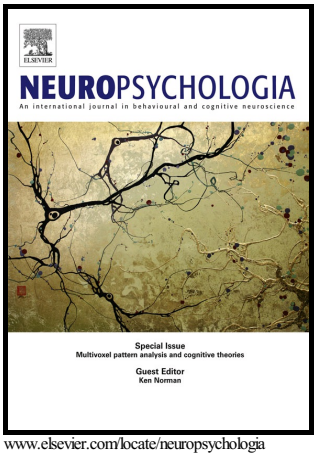

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TMS over right OFA affects individuation of faces but not of exemplars of objects

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Abstract

In addition to its well-documented role in processing of faces, the occipital face area in the right hemisphere (rOFA) may also play a role in identifying specific individuals within a class of objects. Here we explored this issue by using fMRI-guided TMS. In a first experiment, participants had to judge whether two sequentially presented images of faces or objects represented exactly the same exemplar or two different exemplars of the same class, while receiving online TMS over either the rOFA, the right lateral occipital cortex (rLO) or the Vertex (control). We found that, relative to Vertex, stimulation of rOFA impaired individuation of faces only, with no effect on objects; in contrast, TMS over rLO reduced individuation of objects but not of faces. In a second control experiment participants judged whether a picture representing a fragment of a stimulus belonged or not to the subsequently presented image of a whole stimulus (part-whole matching task). Our results showed that rOFA stimulation selectively disrupted performance with faces, whereas performance with objects (but not with faces) was selectively affected by TMS over rLO. Overall, our findings suggest that rOFA does not contribute to discriminate between exemplars of non-face objects.

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Introduction

The occipital face area (OFA), located in the lateral inferior occipital gyrus, is a functionally defined face-sensitive area, typically showing a preferential response to faces relative to objects (Gauthier et al., 2000a; Haxby, Hoffman, & Gobbini, 2000; Minnebusch, Suchan, Koster, & Daum, 2009; Rossion et al., 2003; Yovel & Kanwisher, 2005; for reviews, see Atkinson & Adolphs, 2011; Pitcher, Walsh & Duchaine, 2011). Although OFA in the right hemisphere (rOFA) is recognized as a critical component of the "core system" devoted to face processing, its specific role in the face-processing stream remains controversial. Specifically, while several studies indicate a role of this region in the early, lower-level stages of face detection such as analysis of face local parts (e.g., Liu, Harris, & Kanwisher, 2010; Nichols, Betts, & Wilson, 2010; Pitcher, Walsh, Yovel, & Duchaine, 2007; Zhang, Li, Song & Liu, 2012) or the physical structure of the face (Rotshtein et al., 2005), there is evidence that OFA might be also implicated in later stages of face elaboration, like in recognition of face expressions and in identity discrimination (Ambrus, Windel, Burton & Kovács, 2017; Kadosh, Walsh, & Kadosh, 2011; Solomon-Harris, Mullin & Steeves, 2013; Solomon-Harris, Rafique, & Steeves, 2016; Xu & Biederman, 2010).

In addition to its role in face processing, OFA may also be involved in encoding of non-face stimuli (e.g., Bona, Cattaneo & Silvanto, 2015, 2016; Gilaie-Dotan, Nir, & Malach, 2008; Haist, Lee, & Stiles, 2010; Renzi et al., 2015; Silvanto, Schwarzkopf, Gilaie-Dotan, & Rees, 2010; Slotnick & White, 2013). For example, neuroimaging studies have demonstrated a strong OFA response associated to perception of both faces and houses relative to textures (Gilaie-Dotan et al., 2008) as well as a comparable magnitude of activation within this region in response to face and non-face stimuli (abstract shapes) when the latter are presented in specific locations of the visual field (Slotnick & White, 2013). Similarly, when the task explicitly requires to identify specific individuals within a class (*i.e.*, individuation), OFA shows an equivalent activation in response to face and non-face stimuli (Haist et al., 2010). Accordingly, interfering with OFA activity with TMS was found to impair the recognition of two-dimensional meaningless shapes across large rotations (Silvanto et al., 2010) and to disrupt the discrimination of symmetric and non-symmetric dense dot patterns (Bona et al., 2015). In another study, TMS over rOFA affected participants' ability to recognize Mooney faces but also different types of Mooney objects, a class of stimuli missing distinguishable local features which can therefore be identified exclusively based on their

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global/holistic structure (Bona et al., 2016; see also Renzi et al., 2015). **Interestingly, it has been suggested that OFA may function as a gate that provides inputs to downstream cortical sites, and switches its functional connectivity between the object-network and the face-network depending on the task employed (Zhen et al., 2013; see also Zhao et al., 2016). In line with this, comorbid deficits in both face and object recognition have been sometimes reported in congenital prosopagnosia (e.g., Dinkelacker et al. 2011; Johnen et al., 2014; Zhao et al., 2016), a disorder mainly affecting face recognition (for a review, see Behrmann & Avidan, 2005; see also Cattaneo et al., 2016) and that has been associated to altered spontaneous neural activity in OFA (Zhao et al., 2016) and to abnormalities in functional connectivity between OFA and downstream regions, such as FFA (e.g., Zhao et al., 2018; see also, Behrman & Plaut, 2013).**

As mentioned above, prior neuroimaging findings suggest that OFA may be involved in individuation processing of both face and non-face stimuli (Haist et al., 2010). More specifically, in Haist et al. (2010)'s study, participants were presented with pairs of images of either faces or various objects which could represent either the identical exemplar or two different exemplars belonging to the same category (*e.g.*, two images of the same person or two different individuals); participants' task was to judge whether the two stimuli were of the same identity. Critically, such individuation task was shown to induce an equal response within OFA (as well as in another face-sensitive region, the face fusiform area, FFA) across face and object categories, suggesting that, when items need to be processed at the individual level, OFA is activated by non-face stimuli as much as by faces (Haist et al., 2010). **In line with Haist et al. (2010)'s findings, here we used online fMRI-guided TMS (e.g. Sack et al., 2009) to investigate whether interfering with rOFA activity affects individuation** of face and non-face stimuli.

In Experiment 1 we applied TMS over either the rOFA, the right lateral occipital cortex (rLO) or the Vertex meanwhile participants performed an adapted version of the task employed in Haist et al.'s fMRI study (2010). As a control condition (not involving individuation), we carried out a second study using a "part-whole matching task" with the same stimulus categories as in Experiment 1; specifically, participants were presented with a stimulus fragment, followed by an image of a whole stimulus, and required to judge whether the former was part of the entire stimulus or not. This second experiment was carried out to ensure correct localization of OFA: since consistent evidence suggests that rOFA is involved in encoding face parts, we expected TMS over this region to selectively disrupt performance for faces in the control task (e.g., Pitcher et al., 2007). **If rOFA plays a role** in individuation processing irrespective of stimulus category, as suggested by

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prior neuroimaging evidence (Haist et al., 2010), TMS over rOFA should affect both faces and objects individuation in Experiment 1.

Materials and methods

Participants

Nineteen right-handed students (8 males, mean age=23.3, SD=2.08), with normal or corrected-to normal vision were recruited for the study. Prior to participation, all volunteers were screened for contra-indications to fMRI and TMS and filled out a written informed consent. The experimental protocol was approved by the local ethics committee and conducted in accordance with the guidelines of the Declaration of Helsinki. Each participant underwent three sessions (performed in three different days): first the fMRI localization, followed by the two TMS experiments in the second and third session, respectively.

fMRI localization of LO and OFA

A 3T MAGNETOM Skyra whole-body scanner (Siemens Healthcare, Erlangen, Germany) equipped with a 30-channel head-neck coil was used to perform the functional localization. The measurements were carried out using the same procedure as in our previous studies targeting the same brain regions (Bona et al., 2014, 2015, 2016). LO was localized by presenting participants with gray-scale images of intact objects and their scrambled versions, which were created by randomly selecting an equal number of square tiles from the original object images and re-arranging their locations within the picture; for localization of rOFA, images of faces and intact objects were employed. All stimuli were displayed at a viewing distance of 40 cm on a 18-inch monitor (display resolution: 1280x1024). rLO was localized in a single run lasting 432 sec with gradient echo sequence (23 slices with 3.5 mm slice thickness, RT=2 s, echo time= 30 ms, voxel size= 3.125 x 3.125 x 3 mm^3, flip angle= 75) and corresponded **to the activation peak of cluster of voxels** showing greater activation in response to objects rather than scrambled objects. rOFA was localized over 2 runs (each lasting 271 sec) by using the same parameters as for rLO localization and corresponded to **the activation peak of the cluster of voxels** responding more intensively to faces versus objects. During the scan, a high resolution T1 weighted MPRAGE anatomical scan was also collected for each participant, in order to co-register the individual functional data. SPM8

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MatlabTM toolbox (http://www.fil.ion.ucl.ac.uk/spm, cf. Friston et al. 2007) was employed for data preprocessing, parameter estimation and visualization. The first four slices of each run were removed to ensure a T2 stabilization and the subsequent functional images were corrected for slice acquisition order and head movements. During the parameter estimation process, the functional data were high-pass filtered with 128 sec cutoff, and noise autocorrelation was modeled with AR(1) model. The mean MNI coordinates were as follows: *rOFA*: 46 (SD=3.9), -75 (SD=3.8), -5 (SD=7.7); *rLO*: 40 (SD=5.1), -81 (SD=9.1), -9 (SD=4.3) **(see Supplementary Materials for individual MNI coordinates for *rOFA* and *rLO*). Although exact functional localization of OFA and LO may also largely vary among individuals, similar MNI coordinates have been reported in earlier fMRI and fMRI-guided TMS works on the same regions (e.g., Ambrus et al., 2017; Gauthier et al., 2000; Gilaie-Dotan et al., 2010; Moro et al., 2008; Silvanto et al., 2010). For instance, in a fMRI study by Gilaie-Dotan et al. (2010), MNI coordinates for rOFA were x: 46; y: -80, z: -5, quite similar to the ones we reported.** Figure 1 shows the rOFA and rLO sites in a representative participant.

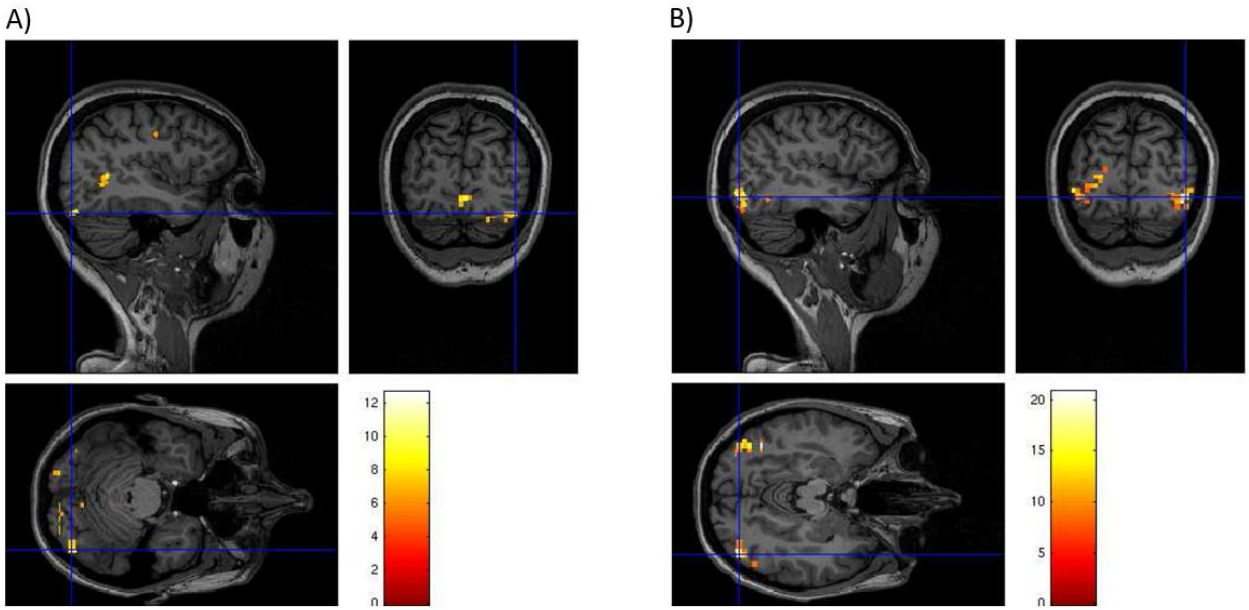

Figure 1. Axial, sagittal and coronal view (from lower left in clockwise order) of the location of the rOFA (A) and rLO (B) in a representative participant.

TMS stimulation

A Nextim stimulator (Nextim Ltd, Helsinki, Finland) connected with biphasic figure-of-eight coil was used to administer TMS pulses. The functionally localized stimulation sites (rLO and

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rOFA) were targeted on each participant using Eximia NBS neuronavigation system (Nextim Ltd, Helsinki, Finland), a co-registration software which allows real-time fMRI-guided positioning of the coil with a spatial resolution of 2 mm (e.g., Hauck et al., 2015; Koivisto et al., 2014). The TMS parameters were the same as in our previous studies targeting the same brain areas (Bona et al., 2015, 2016): specifically, stimulation consisted of 3 TMS pulses, at a frequency of 10 Hz and an intensity of 40% of the maximum stimulator output. A fixed TMS intensity was used consistent with most previous studies assessing OFA's (e.g. Kadosh et al., 2011; Pitcher et al., 2007) and LO's (e.g., Cattaneo et al., 2011, 2015; Mullin & Steeves, 2011; Pitcher et al., 2009) function (for intensity issue in TMS studies see Silvanto & Cattaneo, 2017; Silvanto, Bona, & Cattaneo, 2017). The pulses were delivered over the stimulation sites concurrently with the "probe" onset (see next paragraph). The stimulation was administered by placing the coil tangentially over the activation peaks obtained during the fMRI localization with the coil handle pointing upwards and parallel to the sagittal midline (e.g., Kadosh et al., 2011; Pitcher et al., 2012).Vertex was localized as the halfway point between the inion and the nasion and equidistant from left and right intertragal notches (Dilks, Julian, Paunov, & Kanwisher, 2013; Pitcher et al., 2007) and was included as a control site to ensure that the TMS effects were not due to auditory and somatosensonsory sensation of the pulses.

Experimental tasks:

Experiment 1: Individuation of faces, watches and objects

In Experiment 1 participants performed an individuation task, namely they judged whether two sequentially presented stimuli belonging to the same class (*e.g.*, two faces) represented either the identical exemplar (*i.e.*, they were of same identity, for example two images of the same person) or two different exemplars of the same category (*e.g.*, images of two different individuals).

Stimuli: Stimuli were selected from the original set of Haist et al. (2010) and consisted of 36 images: 12 faces (6 male and 6 female), 12 wristwatches (6 analogic and 6 digital) and 12 various objects (e.g., cameras, cups, keys, teapots). Figure 2A shows an example of each stimulus type. Wristwatches were originally used by Haist et al. (2010) as a distinct set of specific stimuli to be compared to faces because they are similar to faces in that they are both a highly homogeneous class exhibiting a prototypical shape. **Although several studies on face processing present faces with no visible hair (e.g., Pitcher et al., 2009; Renzi et al., 2013), we maintained the hair visible to keep the stimuli identical to those used by Haist et al. (2010) (note that other TMS**

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studies related to face processing maintained hair visible, e.g., Pitcher et al., 2011; Campanella et al., 2013). For each stimulus, two perceptually non-identical versions (*i.e.*, with minor changes in the view point or in the lighting conditions, or with slightly different face expression in the case of faces; see Haist et al., 2010) were created and employed in the "same" trials.

Procedure: The timeline of an experimental trial is illustrated in Figure 2B. Stimuli were presented centrally on a 18-inch monitor with a display resolution of 1600x1200 and participants sat with their heads stabilized on a chinrest at a viewing distance of 60 cm. The software E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) was used for stimulus presentation, data collection and TMS triggering. Each trial began with a black fixation cross appearing for 100 ms, followed by a 500 ms blank screen, and the presentation of the first stimulus ("target"). A blank screen was then presented for 300 ms, followed by the second stimulus ("probe"). In Faces and Objects blocks, both target and probe were displayed for 50 ms, whereas in Watches blocks they both remained visible for 100 ms, in order to reach a similar accuracy level (80-90%) across the three different stimulus categories. These durations were chosen on the basis of a previous behavioral pilot. Participants were instructed to indicate whether the "probe" stimulus represented either the same exemplar as the "target" stimulus (*i.e.*, they had same identity, "*same*" trials) or another exemplar belonging to the same category (*i.e.*, they had different identity, "*different*" trials). The response was provided with a button press (participants used their right index and middle finger to respond) and both accuracy and response speed were stressed. On each trial, a TMS train (3 pulses at 10 Hz, *i.e.* pulse gap of 100 ms) was delivered concurrently with the onset of the probe over the rLO, the rOFA or Vertex (baseline). Note that in "*same*" trials the two stimuli represented the same exemplar but the images were not perceptually identical (see "stimuli" section) in order to ensure participants could not rely on low-level matching strategies. Also, in the "different" trials, target and probe represented two different exemplars but always belonging to exactly the same category (*e.g.*, in the face blocks, a female face was paired with a different female face as well as a male face was paired with a different male face; in the watch blocks, a digital watch was paired with a different digital watch and an analogical watch was paired with a different analogical watch). Importantly, in the "object" blocks although various objects were presented across the block, on each trial the two stimuli represented either the same object exemplar (e.g. the same cup) or two different exemplars of the same object (*i.e.*, two different cups). The task was thus identical across the three different

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stimulus categories and required to distinguish one individual exemplar from another of the same category. The different stimulus categories (faces, watches and different objects) were tested in different blocks, of which participants were informed in advance. For each stimulus category (faces, watches and objects) participants carried out three blocks, that is one block for each stimulation site (rLO, rOFA, and Vertex). Therefore, nine blocks were performed in total. A single block consisted of 64 trials (32 "same" trials and 32 "different" trials, randomly presented). The order of TMS blocks and the order of stimulus categories was randomized across participants, with the constraint that the three blocks of each stimulus category were always performed in a raw, before moving to the following category. Prior to the experiment, participants underwent a brief practice session (with no TMS) for each stimulus category consisting of 20 trials (10 "same" trials and 10 "different" trials).

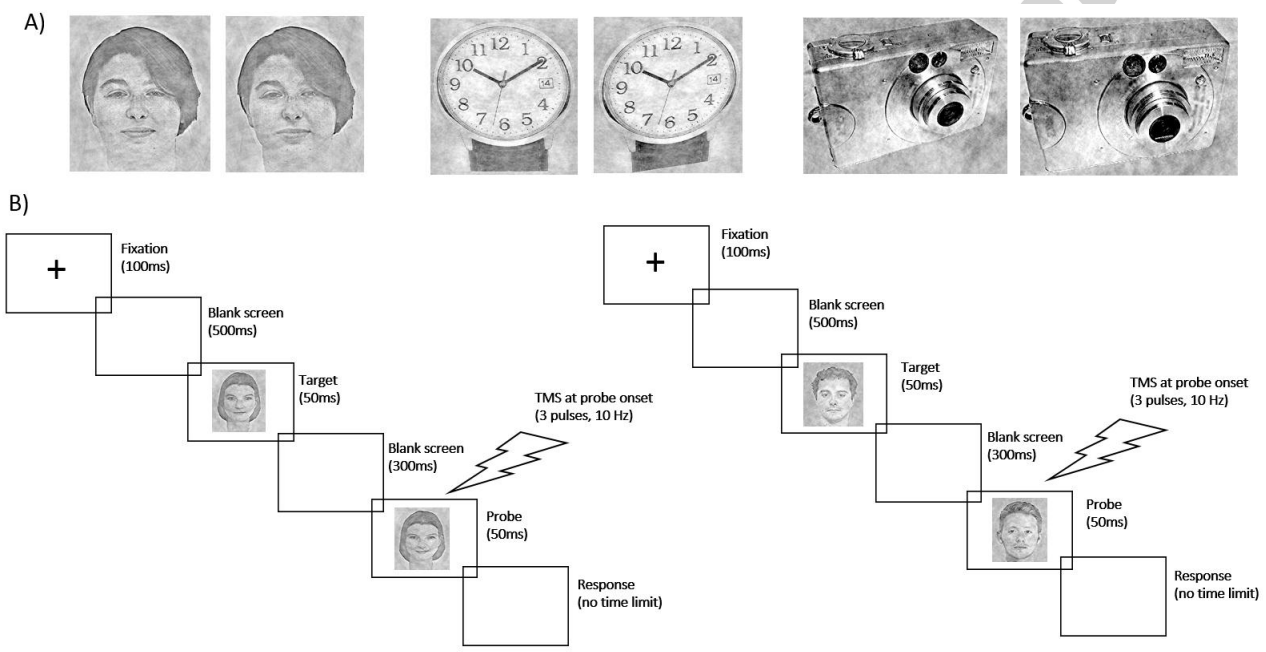

Figure 2. A) Examples of two perceptually non-identical versions of an exemplar from each of the three stimulus categories (used for "same trials") employed in Experiment 1. **B)** Timeline of an experimental trial: on each trial, participants had to indicate whether the stimulus target and the stimulus probe were either identical, *i.e.*, they had the same identity ("same" trials, left panel) or represented two different exemplars of the same class ("different" trials, right panel). Faces, watches and various objects were tested in different blocks. TMS stimulation (3 pulses, 10 Hz) was delivered concurrently with presentation of the probe.

Experiment 2: Part-whole matching task with faces, watches and objects

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In Experiment 2, participants judged whether a stimulus fragment either belonged to a whole stimulus presented immediately afterwards or belonged to another exemplar of the same class.

Stimuli: The stimuli were the same as in Experiment 1. For each image, we generated the "target" stimuli (see next section) by sectioning a local fragment from the original image and presenting it in isolation (see Figure 3A for an example). The stimulus fragments were rectangular patches of different size but all containing a highly informative stimulus feature (e.g., an eye, nose or mouth for faces; a digit for the watches; and an identifiable piece for the objects, such as an handle). For each stimulus of the three categories, four different fragments were created.

Procedure**:** The timeline of an experimental trial is shown in Figure 3B. The procedure was the same as in Experiment 1 with the exception that the "target" stimulus consisted in a stimulus fragment (e.g., an eye in the experimental block with face stimuli) and the "probe" stimulus consisted in the whole stimulus (e.g., one entire face). Participants had to indicate, with a button press (using their right index and middle finger), whether the stimulus part belonged to the subsequent whole stimulus or did not (*i.e.*, belonged to another stimulus of the same class; *e.g.*, in face blocks, an eye that could be part of the whole face presented afterwards or part of another face). Faces, watches and objects were tested in different blocks, of which participants were informed in advance. All stimuli (both targets and probes) appeared on the screen for 100 ms: this duration was chosen on the basis of a behavioural pilot in order to reach a similar baseline performance as in Experiment 1 (80-90%). Both TMS site and stimulation parameters were the same of Experiment 1. Each participant carried out three blocks for each category, one for each stimulation site (rOFA, rLO and Vertex). Each block contained 64 trials (32 with the target belonging to the probe and 32 not belonging, presented in random order). Prior to the experiment, participants performed a brief practice (with no TMS) consisting of 20 trials for each category (10 with the target belonging to the probe and 10 not belonging).

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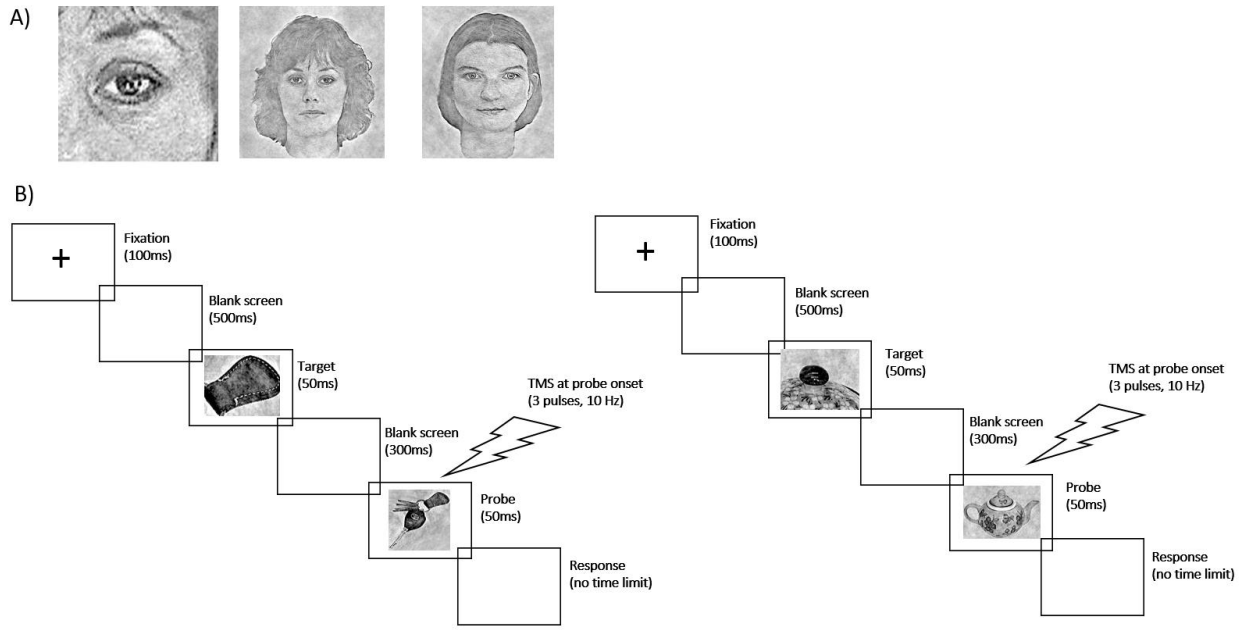

Figure 3. A) Examples of the stimuli used in Experiment 2. The stimulus local fragment is either part of the subsequent whole image or part of another exemplar of the same stimulus class, respectively. **B)** Timeline of an experimental trial: on each trial, participants had to indicate whether the stimulus target belonged to the subsequent whole image or not. Faces, watches and various objects were tested in different blocks. TMS stimulation was delivered concurrently with presentation of the probe.

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Results

Overall performance level was high in all experiments. Mean accuracies were as follows: *Experiment 1 (Individuation task):* 93% (SD =4.94) for faces, 90% (SD =6.47) for watches, and 82% (SD =3.19) for objects; *Experiment 2 (Part-whole matching):* 88% (SD =5.83) for faces, 90% (SD =4.23) for watches, and 93% (SD =5.78) for objects. To take into account possible trade-off effects between participants' RT and accuracy, we carried out statistical analyses on mean reaction times adjusted for accuracy level (*i.e.*, inverse efficiency= mean RT/proportion of correct responses) (e.g., Chambers, Stokes, & Mattingley, 2004; Pavani, Ladavas & Driver, 2002, and as used in our previous studies on rOFA and rLO function, Bona et al., 2014, 2015).

A 3x3x2 repeated-measures ANOVA on mean (adjusted) RT with TMS site (rLO, rOFA,Vertex), Category (Faces, Watches, various Objects) and Task (Individuation, Control) as within-subjects factors showed a significant main effect of TMS site, $F(2,36)=5.37$, $p=.009$, $\eta_p^2=.23$, a significant main effect of Category, $F(2,36)=26.17$, $p<.001$, $\eta_p^2=.59$, and a significant

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main effect of Task, $F(1,18)=8.76$, $p=.008$, $\eta_p^2=.33$. The interactions TMS site x Category, $F(4,72)=10.01$, $p<.001$, $\eta_p^2=.36$, and Category x Task, $F(2,36)=13.63$, $p<.001$, $\eta_p^2=.43$, were significant. The interactions TMS site x Task, $F(2,36)=1.09$, $p=.35$, $\eta_p^2=.06$, and TMS site x Category x Task, $F(4,72)=1.77$, $p=.14$, $\eta_p^2=.09$, were not significant. *Post-hoc t*-tests (Bonferroni–Holm correction applied) on the main effect of Category show that overall performance with various objects was higher than performance with both faces, $t(18)=7.19$, $p<.001$, and watches $t(18)=5.73$, $p<.001$, and performance with watches was significantly higher than performance with faces, $t(18)=2.16$, $p=.045$. The main effect of Task was due to participants being overall slower in the individuation than in the control task; however this effect was modulated by the Category as suggested by the significant interaction Task x Category. *Post-hoc t*-tests (Bonferroni-Holm correction applied) revealed that participants found the individuation task more difficult than the control task particularly with faces, $t(18)=4.94$, $p<.001$, with a similar tendency for the watches' category, $t(18)=2.32$, $p=.064$, whereas performance across the two tasks was similar for objects, $t(18)=1.66$, $p=.114$.

The significant main effect of TMS and the significant TMS x Category interaction were analyzed by looking at the simple main effect of TMS within each Category (Faces, Watches, various Objects), separately. In the *Face Condition*, the ANOVA revealed a significant main effect of TMS, $F(2,36)=12.67$, $p<.001$, $\eta_p^2=.41$. *Post-hoc* comparisons (Bonferroni–Holm correction applied) indicated that performance was significantly impaired when stimulation was applied over rOFA compared to Vertex, $t(18)=3.48$, $p=.006$, and compared to rLO, $t(18)=3.97$, $p=.003$. TMS over rLO did not affect performance compared to Vertex stimulation, $t(18)=1.32$, $p=.204$. In the *Watches Condition*, the ANOVA revealed a significant main effect of TMS, $F(2,36)=16.36$, $p<.001$, $\eta_p^2=.48$. *Post-hoc* comparisons (Bonferroni–Holm correction applied) indicated that TMS over rLO significantly impaired performance compared to Vertex stimulation, $t(18)=4.49$, $p<.001$, and to rOFA stimulation, $t(18)=4.39$, $p<.001$. Performance did not differ between rOFA and Vertex stimulation, $t(18)=.99$, $p=.33$. In the *Objects Condition*, the ANOVA revealed a significant main effect of TMS, $F(2,36)=3.56$, $p=.04$, $\eta_p^2=.16$. Although the pattern was similar to that observed in the watches condition, with TMS over rLO overall impairing performance compared to TMS over the two other sites, the difference failed to reach (Bonferroni-Holm corrected) significance: rLO vs. Vertex, $t(18)=2.17$, $p=.129$; rLO vs. rOFA, $t(18)=1.91$, $p=.144$. Performance in the objects block was similar for TMS over rOFA and over Vertex, $t(18)=.51$, $p=.62$.

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Note that the pattern of TMS effects emerging from analyses on adjusted RT is confirmed by additional similar analyses carried out separately on accuracy scores and reaction times (see Supplementary Materials).

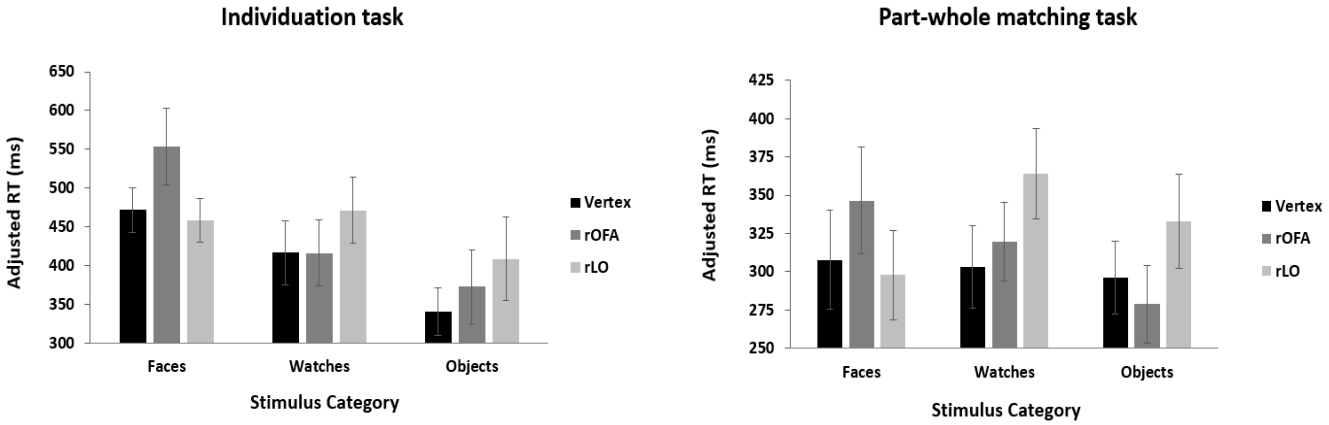

Fig.4 The mean (N=19) adjusted RT (*i.e.*, mean RT/accuracy) for each TMS condition and each stimulus category in Experiment 1 (left panel), which assessed individuation of faces, watches and various objects and in in Experiment 2 (right panel), consisting in a part-whole matching with the same categories used in Experiment 1. In both experiments, relative to Vertex stimulation, TMS over rOFA impaired performance exclusively with faces, but had no impact on performance with watches and various objects; on the other hand, stimulation of rLO reduced performance with watches and objects but not with faces. Error bars represent ±1 SEM.

Discussion

The aim of the present study was to explore **whether interfering with rOFA activity affects** individuation (i.e., discrimination of individual exemplars within a category) of faces of different individuals as well as of different types of objects, as suggested by prior neuroimaging evidence (Haist et al., 2010). Participants were asked to judge whether two sequentially presented images of faces, watches or various objects (tested in different blocks) depicted the same exemplar or two different members of the same class, while receiving fMRI-guided TMS over either the rOFA, the rLO or over Vertex as a control site (Experiment 1). We found that stimulation of rOFA disrupted individuation of faces only, with no effect on objects; on the other hand, interfering with rLO activity impaired individuation of objects, but had no impact on individuation of faces. Correct functional localization of rOFA and rLO was ensured by a control experiment (Experiment 2), in which participants were engaged in a part-whole matching task with faces and objects. TMS over

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rLO in this task selectively affected performance with objects, and TMS over rOFA selectively affected performance with faces, as expected on the basis of the well-known role of rOFA in the analysis of local face parts (e.g., Pitcher et al., 2007).

In a prior neuroimaging study, Haist et al. (2010) found that when the task required to distinguish between individual exemplars of the same class, OFA (as well as FFA) showed a comparable response regardless of whether the stimuli were faces or objects. These findings were interpreted as suggesting that OFA and FFA may not be strictly face-specific regions, being also implicated in individuation of members of other stimulus categories (Haist et al., 2010). Haist et al (2010)'s findings relate to a series of earlier fMRI results by Gauthier and colleagues showing activity in OFA and FFA during discrimination of both faces and objects and suggesting that these regions may mediate encoding of stimuli at a subordinate level (i.e., at the level of individuals), irrespective of stimulus identity (e.g., Bukach et al., 2012; Gauthier et al., 1997, 1999, 2000b; Gauthier & Tarr, 2002; Tarr & Gauthier, 2000). Gauthier et al.'s noted though that OFA and FFA responses reflected observers' expertise with the stimuli presented: indeed, FFA was found to show a robust response to birds and cars only in participants who were expert in these classes of stimuli (Gauthier et al., 2000b; but see Grill-Spector, Knouf, & Kanwisher, 2004); and individuation of unfamiliar, meaningless objects (Greebles) elicited stronger OFA and FFA responses in participants who underwent a previous training with these stimuli, relative to untrained participants (Gauthier & Tarr, 2002; Gauthier et al., 1999, 2000; Tarr & Gauthier, 2000).

The lack of rOFA TMS effects we reported in our study with objects do not support the view that rOFA is critically involved in distinguishing between exemplars of non-face stimuli. In our study we used highly familiar objects (such as watches, cups, etc), so it is also unlikely that lack of OFA-TMS effects on objects individuation depended on participants' lacking expertise with the stimuli. In a recent TMS study, we found that OFA **is involved in** detection of vertical but not horizontal symmetry in dot configurations (Cattaneo, Bona & Silvanto, 2017), and we suggested that OFA's role in encoding vertical symmetry might depend on this region being critically involved in encoding of faces, for which (vertical) symmetry represents a critical cue (e.g., Anderson & Gleddie, 2013; Chen, Kao & Tyler, 2007; Rhodes et al., 2005). An important role of symmetry in driving OFA activation has also been suggested by Silvanto et al. (2010)'s work, revealing that this regions is causally involved in discrimination of symmetrical 2D shapes when presented at large rotations. In line with the above, OFA recruitment during processing of non-face

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stimuli may depend on the extent to which features to be processed (such as symmetry, rotation invariance, etc) are also important for face processing.

The face individuation task we used required participants to evaluate whether two sequentially presented faces represented the same person or two different individuals, forcing them to explicitly focus on face identity. Critically, while the FFA is most commonly implicated in face individuation (e.g., Andrews & Ewbank, 2004; Gauthier et al., 2000a; Grill-Spector et al., 2004), some reports have also found significant adaptation effects within OFA in response to repeated presentation of different images of the same individual (e.g., Andrews, Baseler, Jenkins, Burton, & Young 2016; Gauthier et al., 2000b; Pourtois et al., 2005; Xu & Biederman, 2010). Accordingly, Kadosh et al. (2011) found that interfering with OFA via TMS reduced the ability to detect variations in identity (as well as in face expressions) in two sequentially presented faces; and Ambrus et al. (2017) showed that TMS over OFA impaired learning of novel face identities**. If on one hand our data are in line with studies claiming for some identity-sensitivity in OFA, on the other hand it is known that TMS over a targeted region may affect brain connectivity and networks (for a recent review, see Hallett et al., 2017). Accordingly, by combining TMS with fMRI Solomon-Harris et al. (2016) have recently shown that deep regions within the face network, such as FFA and the posterior superior temporal sulcus, can be remotely probed by stimulation of OFA. It may thus be that our stimulation affected functional connectivity between OFA and FFA, rather than activity in OFA *per se*. In this view, it is interesting that development disorders of face recognition (prosopagnosia) have been associated to both neural-processing abnormalities in FFA and/or OFA (e.g., Minnebusch et al., 2009; Zhang et al., 2015; Zhao et al., 2016), and to functional dysconnectivity between early visual cortex, OFA and FFA (e.g., Zhao et al., 2018;see also, Behrman & Plaut, 2016; Lohse et al., 2016).**

In sum, our findings – **either resulting from selective stimulation of OFA or from more diffuse network effects** - suggest **that interfering with OFA activity** affects individuals' capacity to discriminating among exemplars of faces but not among exemplars of different objects. Future studies are needed to further define the functional profile of OFA, exploring whether under specific circumstances this region may also be involved in objects' individuation as suggested by prior neuroimaging evidence (Haist et al., 2010; see also Zhao et al., 2016).

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Highlights

- TMS over rOFA affected faces but not objects individuation
- TMS over rLO affected objects but not faces individuation
- rOFA does not contribute to discriminate between exemplars of non-face objects

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